The Structure and Possible Function of the Spiracles of some Scolopendridae (Chilopoda, Scolopendromorpha)

*John G. E. LEWIS *, Trevor J. HILL * & Gavin E. WAKLEY ***

* Taunton School, Taunton, Somerset TA2 6AD, U. K.
** Department of Biological Sciences, Washington Singer Laboratories, University of Exeter, Perry Road, Exeter EX4 4QG, U. K.

ABSTRACT

The results of a scanning electron microscope investigation into the structure of the spiracles of four species of scolopendrid centipedes are reported. *Rhysida nuda togoensis* (Kraepelin), *Ethmostigmus trigonopodus* (Leach), *Scolopendra morsitans* L., *Scolopendra valida* Lucas, were studied. The spiracles serve to prevent debris entering the tracheal system. The relatively simple spiracles of *Rhysida* and *Ethmostigmus* may function as a plastron in small specimens. The more complex spiracles of *Scolopendra* spp. may function principally to prevent water loss, although it is possible that the large sub-atrial cavities in *S. morsitans* may form a plastron. *R. nuda* and *E. trigonopodus* are absent from arid habitats.

RÉSUMÉ

Structure et fonction probable des spiracles de quelques Scolopendridae (Chilopoda, Scolopendromorpha).

L'ultrastructure des spiracles de Scolopendridae est étudiée chez *Rhysida nuda togoensis* (Kraepelin), *Ethmostigmus trigonopodus* (Leach), *Scolopendra morsitans* L., et *Scolopendra valida* Lucas. La fonction des spiracles est essentiellement d'empêcher l'entrée de débris dans le système trachéen. Ils sont simples chez *Rhysida* et *Ethmostigmus*, qui manquent dans les habitats arides, et fonctionnent comme plastron chez les petits individus. Plus complexes chez *Scolopendra* sp., ils pourraient fonctionner comme préventifs du dessèchement, bien qu'il soit possible que la grande cavité sous-atriale de *S. morsitans* forme un plastron.

INTRODUCTION

The literature on the structure of centipede spiracles has been reviewed by VERHOEFF (1941) and LEWIS (1981). Most genera of the order Scolopendromorpha have 21 leg-bearing segments and in these spiracles are present on segments 3, 5, 8, 10, 12, 14, 16, 18 and 20 and sometimes 7.

In genera with 23 leg-bearing segments spiracles are, in addition, present on segment 22. The genus *Plutonium* is unusual in having spiracles on every leg-bearing segment except the first and last.

The scolopendromorphs show a considerable variation in spiracle structure. In the family Cryptopsidae the elliptical spiracle in *Cryptops* leads to the atrium which itself opens by a

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crescent-shaped slit into a subatrial cavity (FÜLLER, 1960): both cavities are lined by trichomes. In *Otocryptops* the atrium is funnel-shaped and there is no subatrial cavity (VERHOEFF, 1941). The two subfamilies of the Scolopendridae are distinguished by the structure of their spiracles. In the Otostigminae the spiracles are mostly rounded and without valves (Fig. 1A) whereas the Scolopendrinae have triangular spiracles with three-flapped valves (Fig. 3A).

MATERIALS AND METHODS

Four species have been investigated using the scanning electron microscope, namely: *Rhysida nuda togoensis* Kraepelin, *Ethmostigmus trigonopodus* (Leach) and *Scolopendra morsitans* L., all from Nigeria, and *Scolopendra valida* Lucas from Oman.

The material, which had been preserved in 70 per cent ethanol, was dehydrated in absolute ethanol for at least 24 hours and then air dried, sputter coated with gold and then examined in a Cambridge 100S scanning electron microscope. Preparations for examination under the light microscope were mounted in Hoyer's mountant.

RESULTS

Subfamily Otostigminae

Rhysida nuda togoensis Kraepelin

The spiracles of *Rhysida* are approximately elliptical (Fig. 1A), the axis of the ellipse sloping obliquely forwards and upwards on segment 3 but more or less vertical on the posterior spiracles, the lower border less curved than the upper. The first spiracle, is almost twice the length of the subsequent ones. The peritrema is scalloped. The atrial wall is thrown into a number of vertical ridges and the floor into humps (Fig. 1B, C). The atrial surface is covered by complex trichomes which are of variable shape. Those immediately beneath the peritrema have angular heads but most are elongated. The sides show a reticulate strutting so that they are honey-combed with cavities (Fig. 1D). The ridge-like trichomes are 11 µm high, 10-14 µm long and 1.25-2.50 µm wide. The wide tracheae open between the humps of the atrial floor. Their openings are surrounded by digitate trichomes whose surfaces are covered by a network of ridges (Fig. 1E). They are 60 µm long and are here termed guard hairs.

Ethmostigmus trigonopodus (Leach)

The general structure of the spiracle of *Ethmostigmus (=Heterostoma)* was accurately described by HAASE (1884) and by VERHOEFF (1941). As in *Rhysida* the spiracles are approximately elliptical but the first spiracle (Fig. 2A) is particularly large and the atrium saucer-shaped, its floor being only slightly below the level the surrounding stigmatopleurite (Fig. 5A). The subsequent spiracles become progressively more bowl-like and in small specimens resemble those of *Rhysida*. The floor of the spiracle (Fig. 2B) is thrown into large humps or ridges covered with trichomes. Those on top of the humps have scalloped heads 7-12 µm across (Fig. 2C). These were described as six-pointed stars by VERHOEFF. The sides and bases show reticulate strutting (Fig. 2E). The trichomes become more elongated towards the base of the humps so that they resemble those of *Rhysida*. The narrow trichomes are 9-11.4 µm long, 1.4-1.8 µm wide and 10 µm high. The tracheae open at the bases of the humps, their openings protected, as in *Rhysida*, by elongated guard hairs 64 µm long (Fig. 2D, E).

Subfamily Scolopendrinae

Scolopendra morsitans Linnaeus

The structure of the spiracle is very similar to that described for *S. cingulata* Latreille by HAASE (1884) and CHALANDE (1885). It is triangular, the apex being anterior (Fig. 3A). The peritrema is scalloped, most lobes having a short seta centrally.

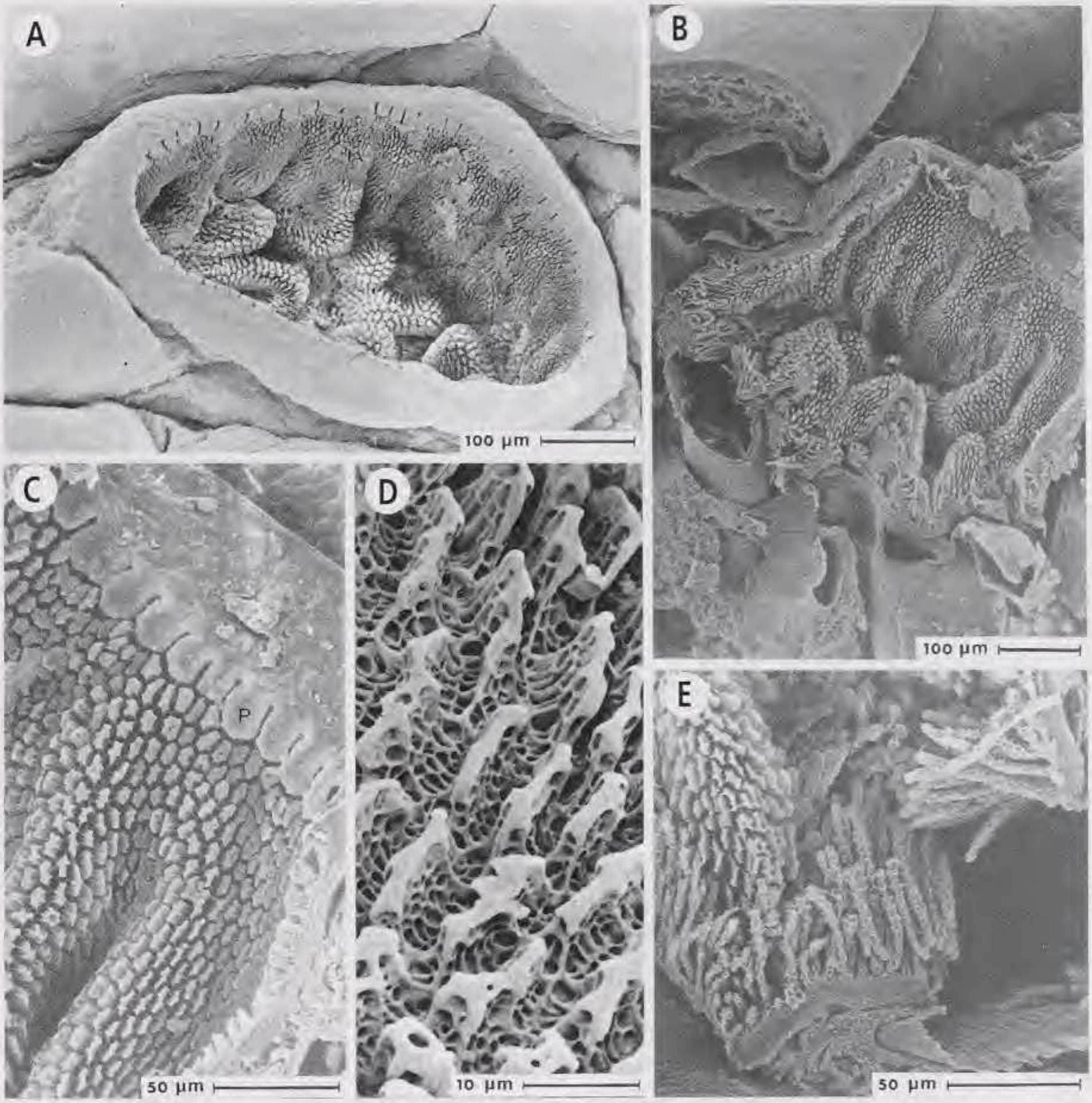


FIG. 1. — *Rhysida nuda togoensis*. Spiracle of segment 3. A. Surface view. B. Vertical section. C. Detail of wall of atrium. P, peritrema. D. Atrial trichomes. E. Guard hairs of tracheal openings.

The atrium is divided into outer and inner cavities by a three flapped valve (Fig. 3B, 5B). The inner atrial cavity is often termed the sub-atrial cavity. Beneath the peritrema the atrial wall bears ridged columnar trichomes 8 µm high, these increase in length towards the valves (Fig. 3D). At the base of the outer atrial cavity there is a row of setose cones (CHALANDE's recumbent plumes) pointing vertically towards the opening of the spiracle (Fig. 3B, C). On the spiracle of segment three there are 8 on the posterior valve and 21-22 on the dorsal and ventral valves. They are about 100 µm high and the longest setae or bristles are 41 µm long. They fill much of the outer atrial cavity, having but a narrow Y-shaped aperture between them. Beneath the row of cones is a band of vertically ridged cuticle devoid of trichomes which forms a valve. The subatrial cavity is extensive, with deeply folded walls covered with trichomes (Fig. 5B). These are 4.6 µm high, their irregularly pitted heads measuring about 6 µm across. The sides show reticulate strutting which is continued on the atrial floor between the trichomes (Fig. 3E). The tracheae open into the floor and sides of the inner atrial cavity, their openings being surrounded by guard hairs like those of *Rhysida* and *Ethmostigmus* (Fig. 3F). These are about 40 µm long.

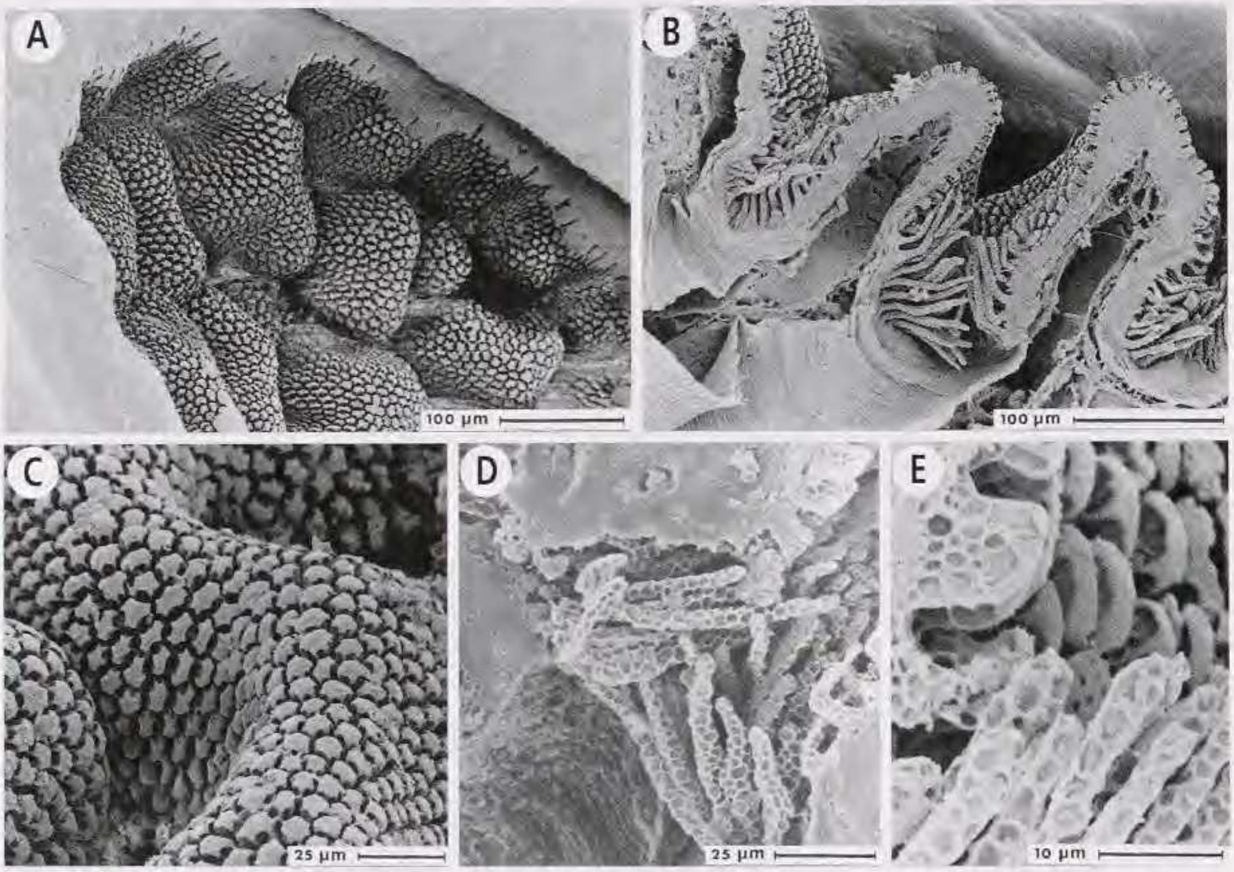
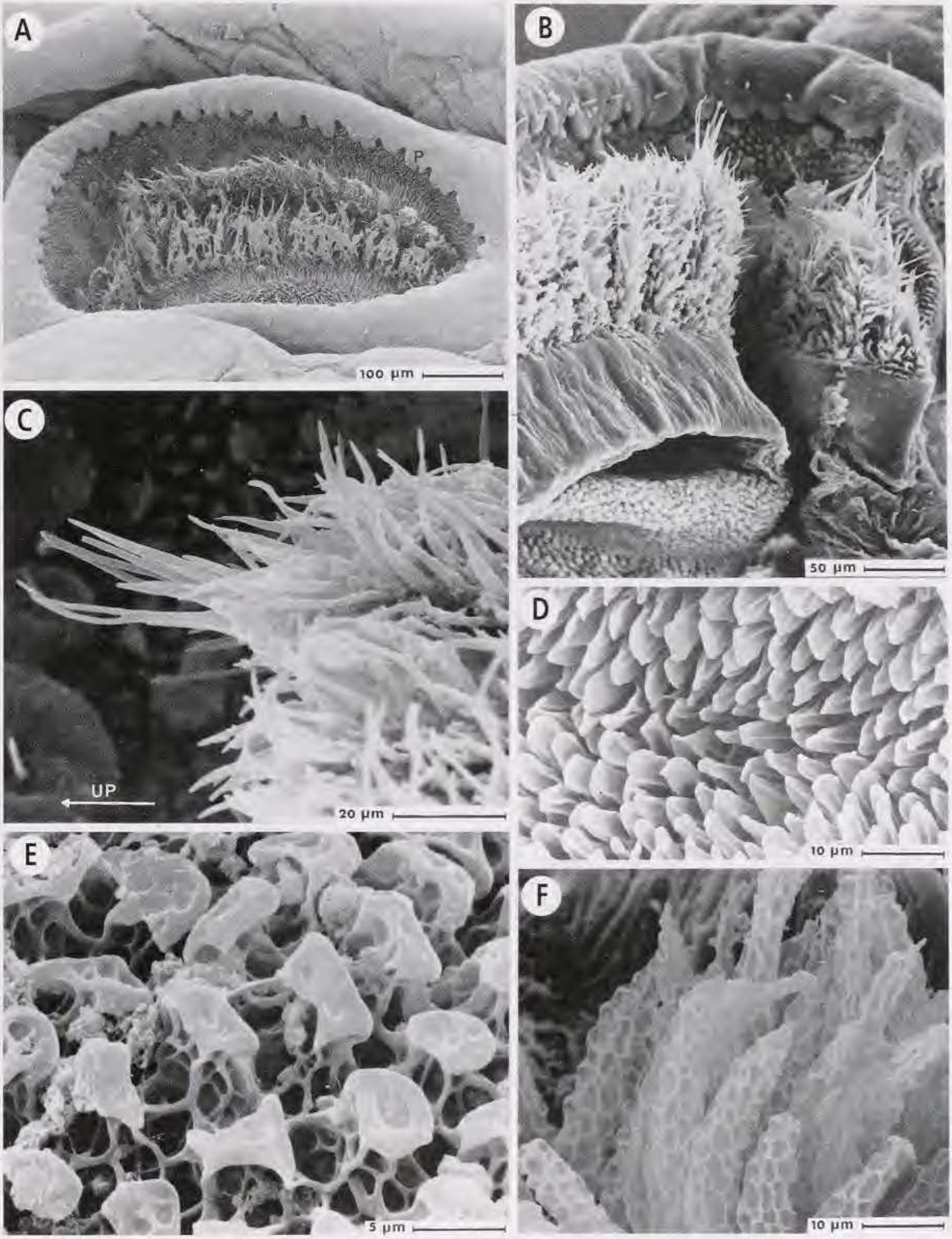


FIG. 2. — *Ethmostigmus trigonopodus*. Spiracle of segment 3. A. Surface view. B. Vertical section (detail). C. Surface view of atrial trichomes. D. Guard hairs of tracheal opening. E. Detail of guard hairs and trichomes.

Scolopendra valida Lucas

The spiracle of *S. valida* (Fig. 4A) resembles that of *S. morsitans* in shape and its division into an outer and inner atrial cavity. The wall of the outer atrial cavity bears trichomes similar to those of *S. morsitans* (Fig. 4B, C). The setae are, however, not borne on cones but form a dense strip along the top of each valve. The valves are composed of trichome free cuticle (Fig. 4D). The inner atrial cavity is not enlarged like that of *S. morsitans* and lacks trichomes. The tracheae open into the chamber, their openings being surrounded by guard hairs 60 µm long.

FIG. 3. — *Scolopendra morsitans*. Spiracle of segment 3. A. Surface view. B. Vertical longitudinal section. C. Setose cone. D. Trichomes of outer atrial cavity. E. Trichomes of inner atrial cavity. F. Guard hairs.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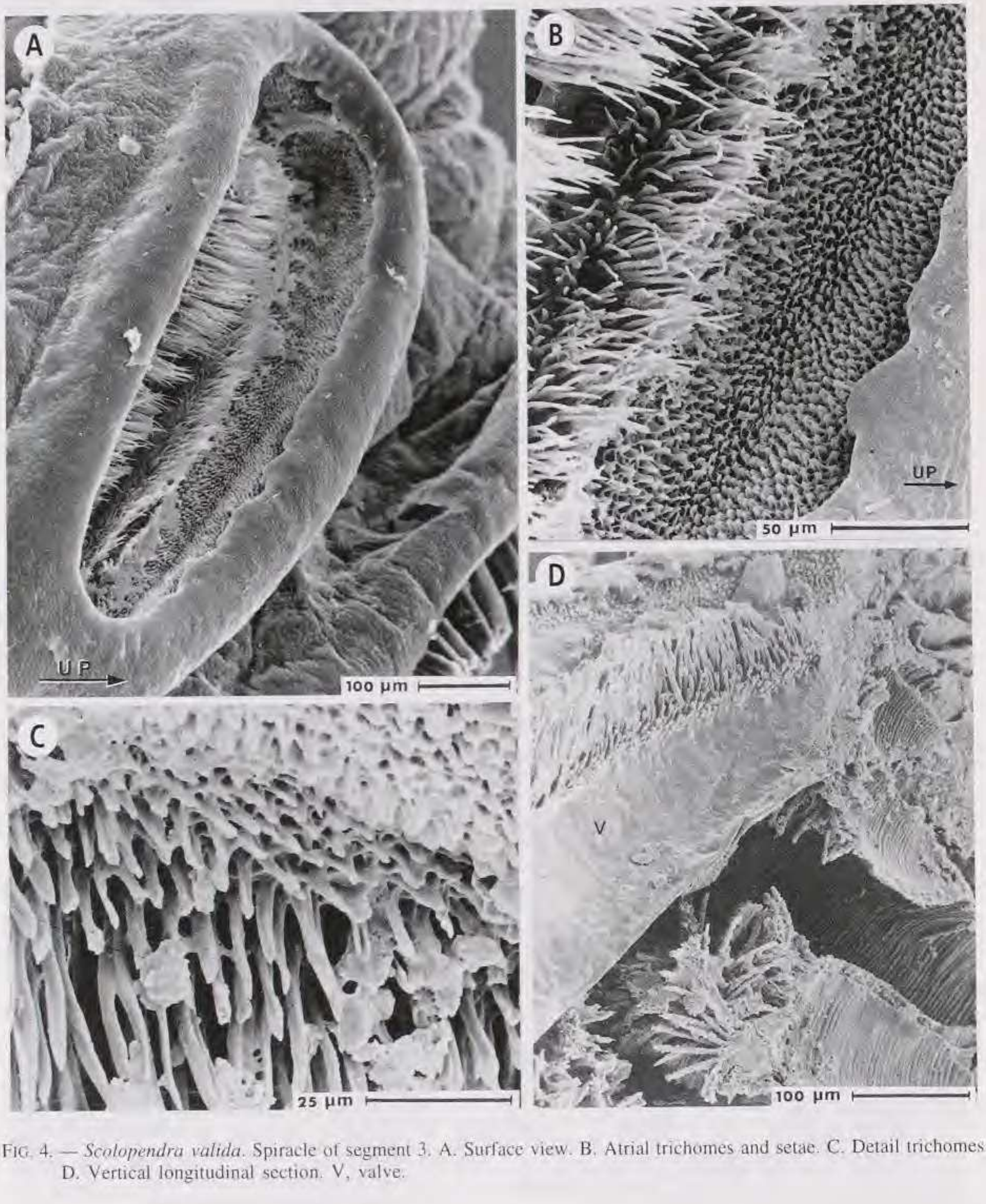

FIG. 4. — *Scolopendra valida*. Spiracle of segment 3. A. Surface view. B. Atrial trichomes and setae. C. Detail trichomes. D. Vertical longitudinal section. V, valve.

DISCUSSION

Spiracles function to reduce water loss from the tracheal system under dry conditions and, in arthropods that experience immersion in water, they frequently act as plastrons. The trichomes may be involved in both these processes. Other functions that have been suggested for spiracular trichomes are that they filter out dust (KAUFMANN, 1962) and prevent spiracular occlusion during locomotion (CURRY, 1974). PUGH *et al.* (1991) suggested that the peritreme of holothyrid mites might prevent suffocation during immersion or act as a water trap.

Spiracular function in Otostigminae

Water loss from the tracheal openings of *Rhysida* and *Ethmostigmus* may be impeded by the spiracular guard hairs which will also prevent debris entering the tracheae. The crevices between the humps of the atrial floor will also retain humid air. It is difficult to visualise a role for the trichomes in this respect as gases diffusing in and out of the tracheae will pass over them rather than between them. A more likely function is that they form a plastron, retaining a layer of air when the centipede is immersed in water as may happen during the rainy season.

HINTON (1968) determined the basal limit of plastron efficiency for insects in terms of the ratio between the area of the plastron and the wet body weight as $1.5 \times 10^4\ \mu m^2.mg^{-1}$. Assuming that the air-water interface is across the tops of the trichomes, a conservative estimate for this ratio for a large specimen of *R. nuda togoensis* length 74 mm, mass 1080 mg is $3.75 \times 10^3\ \mu m^2.mg^{-1}$: well below HINTON's figure. For a small specimen body lēngth 13 mm, mass 11 mg the figure is $1.5 \times 10^4\ \mu m^2.mg^{-1}$, equal to HINTON's minimum value. In an *E. trigonopodus* length 88 mm, mass 2700 mg the ratio is $4.2 \times 10^3\ \mu m^2.mg^{-1}$ but in a small specimen length 29.5 mm, mass 91 mg the value is $2.2 \times 10^4\ \mu m^2.mg^{-1}$. It would appear that in both species small but not large specimens may be able to utilise plastron respiration. These calculations assume that the interface is across the tops of the trichomes.

Although the relative area of a plastron decreases with increased mass of the organism, tracheal volume will increase in proportion to increasing mass. The tracheae of large specimens appear to be particularly voluminous and may function as air stores during immersion.

Spiracular function in Scolopendrinae

It is tempting to suggest that the greater complexity of the scolopendrine spiracle, with the atrium divided horizontally by a three-flapped valve and the presence in *Scolopendra* spp. of dense setae above the valves either borne on cones or not, is related to the need to restrict water loss in dry conditions. PUGH *et al.* (1987) described structures similar to the setose cones from the peritrematic groove of the mite *Phaulodinychus repleta* (Berlese). They consist of micropapillae arranged on christmas tree-like structures and termed compound fimbriae. They suggested that the compound fimbriae of *P. repleta* carried out a protective function preventing the entry of foreign/harmful material into the tracheal system rather than supporting an air film. The irregular and spiky compound fimbriae of *Holothyrus coccinella* (Wormersley) cannot support an airfilm but would pierce the air water interface (PUGH *et al.*, 1991). The setae of the setose cones of *S. morsitans* and the setae of *S. valida* clearly act as sieves and are often covered with debris. The setae will clearly reduce diffusion. If their surface is not hydrophobe then dipole-dipole interactions between water molecules and the protein and chitin molecules of the cuticle will allow free diffusion of oxygen and carbon dioxide whilst impeding that of water. The spiracles of the *Scolopendra* species are small and the area covered by trichomes in the atrial cavities is low. The ratio between the area and body mass for a *S. morsitans* length 70 mm, mass 1042 mg is $1.6 \times 10^3\ \mu m^2.mg^{-1}$, lc. An order of magnitude below HINTON's figure. The figure for a *S. valida* length 110 mm, mass 4370 mg is even lower: $3.7 \times 10^2\ \mu m^2.mg^{-1}$. *S. morsitans*, though not *S. valida*, has large sub-atrial cavities lined with trichomes (Fig. 5B). If these were flooded with water it is possible that they would act as a plastron. Currently, however, there are insufficient data to calculate the area involved.

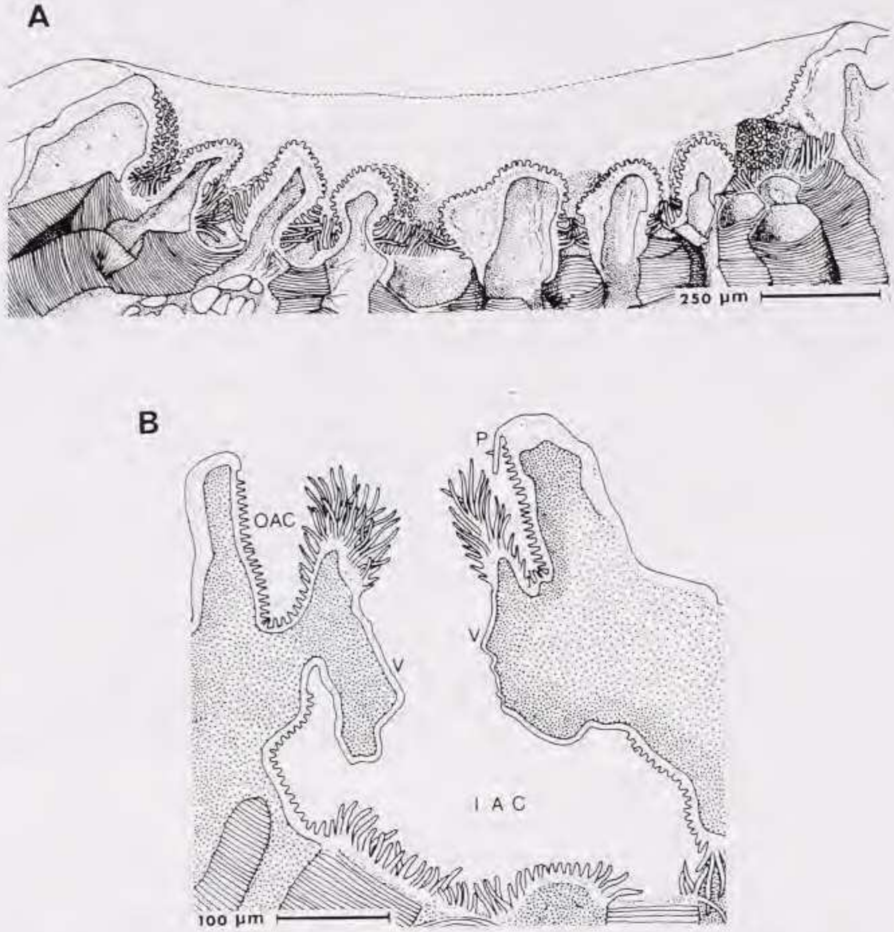

FIG. 5. — A. Vertical longitudinal section of spiracle of segment 3 of *Ethmostigmus trigonopodus*. B. Vertical transverse section of spiracle of segment 3 of *Scolopendra morsitans*. IAC, inner atrial cavity; OAC, outer atrial cavity; P, peritrema; V, valve.

Ecology

Data on the distribution of scolopendrids in West Africa and Saudi Arabia shows that members of the subfamily Scolopendrinae with their triangular spiracles occur in dry and humid regions, whereas members of the subfamily Otostigminae are absent from drier habitats. Thus *Rhysida nuda togoensis* and *Ethmostigmus trigonopodus* are virtually absent from the dry Sudan and Sahel savanna regions of Nigeria (LEWIS, 1972) whereas the scolopendrines *Asanada socotrana* Pocock and *S. morsitans* are widespread there (LEWIS, 1973 and unpublished data).

Rhysida and *Ethmostigmus* have not been recorded from Saudi Arabia but *A. socotrana* and three species of *Scolopendra* (*canidens* Newport, *mirabilis* (Porat) and *valida* Lucas) occur there (LEWIS, 1986).

In the guinea savanna region of Northern Nigeria, *R. nuda* and *E.trigonopodus* are virtually absent from surface habitats during the latter part of the dry season (mid-November to

April) but *S. morsitans* is surface active throughout the year being found under cow dung during the dry season (LEWIS, 1969). The ecological data support the conclusions drawn about possible spiracular functions on the basis of morphological observations.

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